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INTERNAL RELATIONS OF TERRESTRIAL ASSOCIATIONS

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I. INTRODUCTION

THE material here presented is based on the writer's studies, during the past five years, of terrestrial associations of plants and animals, mainly in different parts of the prairie region. The particular area chiefly used for illustration in this paper is the sand prairie of the Illinois River valley, plants and animals of which have been studied by Hart and Gleason (1907) and by the writer (1913*b*). A later study has been made of the vegetation of inland sand areas of Illinois (Gleason, 1910); the Lake Michigan beach area in northeastern Illinois has been studied by Gates (1912); beach areas in Illinois and Indiana by the writer (1914*a*). The chief representation of the sand prairie is the bunch-grass association, well-developed in parts of northwestern, central and northeastern Illinois, and in northwestern Indiana, in each of which areas, as well as in the sandhills of Nebraska and of eastern Colorado, the writer has studied. Discussions of physical, vegetational and animal aspects of the associations of the central Illinois sand prairie, together with an annotated list of the animal species, with data on food, habitat-relations, life-history, etc., are embodied in the writer's paper (1913*b*), to which constant reference is made. Frequent citations to a more detailed study of local distribution of grasshoppers, in a Michigan area (Vestal, 1913*a*), and to the many associational studies of Shelford, are to be found.

The data which have accumulated relate nearly equally to the botanical and zoological aspects of associational study, but since the subject of plant ecology is at present more advanced than that of animal ecology, it has been possible to treat the vegetational side of the problem very briefly, so that more of the discussion relates to animals and animal assemblages.

The writings most frequently cited are indicated by italic capitals, the full titles appearing in the list of special references at the end of the paper.

The writer wishes to thank Dr. Charles C. Adams, Dr. Max M. Ellis and Dr. H. A. Gleason for suggestions and criticism.

II. INTERNAL ACTIVITIES OF THE ASSOCIATION, AS DETERMINED BY THE CONSTITUTION OF THE INDIVIDUAL ORGANISM

The internal activities of the association may be said to be the sum-total of the activities of all the plants and all the animals which make up the association. Such a sum-total of activities may well be thought of as an intricate and complicated mass of dependencies. It will simplify the treatment of the entire system of relations if the chief dependencies of the individual organism are first discussed. A knowledge of the ecology of the association is built up largely from a knowledge of the ecology of all the organisms which compose it.

A. ECOLOGICAL CONSTITUTION OF THE ORGANISM

The constitution of the organism is the sum-total of those of its characters which enter into relation with environment. These are commonly classified as *structural* and *physiological*. For the purposes of this discussion it would seem preferable to subdivide physiological characters, restricting the term *physiological* to denote those characters concerned with ordinary metabolic processes of the organism, and excluding those having to do with life-history and rates of reproduction (these may be distinguished as *biographical* and *numerical*[1]) and also, when dealing with animals, those related to behavior (*psychological* characters). The constitution of the organism in relation to environment will be discussed in terms of these classes of characters.

B. CONSTITUTION OF THE PLANT IN RELATION TO ENVIRONMENT

The environmental influences in the association are of three kinds: (1) physical, (2) plant, (3) animal. Each plant and each animal must obtain from each of these three constituents of its environment certain necessaries; it has certain structural and physiological characters which enable it to obtain these necessaries, and to withstand adverse environmental influences.

The environmental relations of plants are very different from those of animals. A tabular comparison of these relations has been made by Shelford (*A*: 593). As therein pointed out, structural characters are of greatest importance in the adjustment of the plant to the environment, and plants in a given habitat are likely to have a common structure or growth-form, indicating common or ecologically equivalent physiological conditions within.

Different plants (and different animals), within a common habitat, are similar in ecological constitution (ecologically equivalent) in so far as their presence is determined by the same environmental conditions. It should be pointed out that there are local environmental differences within the area of the association which allow the presence of differently constituted organisms, and that the entire range of environmental conditions within the habitat is usually much wider than that of the environmental complex selected by a particular organism. The environmental complex of the organism is not the same as the sum-total of environmental conditions within the association. Each organism differs in greater or less degree from others in ecological constitution, and thus selects a different environmental complex.

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[1] Based partly on Forbes', classification of adaptation to food requirements (1909: 292).

The physical factors of the environment are of greatest importance in the life of the plant. Plants influence one another directly to only a slight extent. There is usually very little of the social relationship among ecologically similar plants which will compare with such relationships as seen in animals. Competition among plants is mainly a struggle to determine which plants are to be most favored by physical conditions, and it is probably most severe for the physical factor present in minimal quantity. In desert associations plant competition is almost exclusively for water, and extensive root systems are developed. In grassland it is very largely for above-ground space; in forests it is principally for light. The influence of the animal-environment is probably of greater importance than has commonly been realized by plant ecologists; the study of economic entomology and of the effects of grazing upon grasslands is helping to bring about a realization of the importance of animal influence upon plant life.

The structures of plants show frequent and great modification in response to the physical conditions of the environment. These modifications are most frequent and important with respect to the factor present in minimal quantity. Characters which may be associated with direct plant influence are infrequent. Certain plants which become more abundant as a result of close grazing are equipped with spines, or have acrid or pungent juices; and many other characters may be correlated with animal influence. The structural modifications are most evident in the adjustment of the plant to external conditions, though these are accompanied by physiological characters which are also in harmony with the environment.

C. CONSTITUTION OF THE ANIMAL IN RELATION TO ENVIRONMENT

The animal, like the plant, selects an environmental complex which is of three kinds: (1) physical, (2) plant, (3) animal. Different animals show extreme variation as to the degree in which the different parts of the environment are important to their existence. Endoparasites, for example, are most directly concerned with the animal part of their environmental complex.

The existence of any animal is dependent upon a number of physical factors, all of which must be present in proper degree or quantity. Minimal and maximal quantities of any one of several factors mark the limits of existence of any animal (*A:* 598—law of toleration of physical factors). It is not necessary to consider these factors in detail. The animal reacts to physical environment most evidently by its behavior: psychological characters restrict activities more narrowly than do those of other types. They are accompanied by structural and physiological characters; hibernation, storage of food, etc., are biographical characters correlated with seasonal changes in physical environment. Animals which are subjected to very severe physical conditions may produce a larger number of offspring than those to which physical conditions are favorable. This is an example of correlation of a numerical character with the physical environment.

The plant environment reacts upon and modifies physical and animal environments, and has also direct influence upon the animal. In addition to its effect in the control of temperature, light and other physical factors, the vegetation constitutes the basic food-supply for the animal community, and also provides shelter and materials for abode (*A:* 601). Cases of direct association between particular plants and particular animals are numerous, but the majority of animals have no direct relation to particular kinds of plants. Behavior characters are in general of greater importance in the relation of the animal to the plant environment, though such relations are not confined to psychological characters.

There are two sets of relations between the animal and its animal environment. These are: (1) *social,* and (2) *antagonistic.* Social relations (*inter-psychology* and *inter-physiology* of Shelford, *A:* 608, *b*) include those between individuals of the same species, and between animals of the same or similar *mores*[2] (ecologically equivalent animals), in so far as these relations are not antagonistic. Breeding and family relations are the principal activities which come under this head. Behavior characters are of greatest importance, as compared with structural and other characters. The antagonistic relations constitute the *intermores-psychology* and *physiology* of Shelford (*A:* 608, *c*). They are the antagonistic relations between animals not ecologically equivalent, and they are also antagonistic relations within a species and between ecologically similar forms. These relations are probably not greatly concerned with reproduction, but center about the feeding activities of the animal. The existence of the individual animal, in its relation to other organisms, is dependent upon three conditions: (1) it must obtain suitable and sufficient food, (2) it must be free from destructive competition of animals of similar requirements, (3) it must be able to escape or to withstand attacks of other animals (or, sometimes, of parasitic fungi or bacteria). The various characters of the animals are correlated with all three of these conditions. The characters are both "adaptive" (fixed by heredity), and regulatory (not fixed).

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[2] *Mores* (Latin for customs, habits) has been used by Shelford (1911*a*: 30) to supply the need for a term including all physiological and behavior characters of the animal.

Following is a synopsis of correlations between the various types of characters and the three conditions of existence, in the relation of the animal to its antagonistic animal environment.

(I) *Characters Which Enable the Animal to Obtain Food*

1. *Structural Characters.*—Animals of selective food-habits often have specialized structures, as in the case of the long tongue of woodpeckers. Animals of non-selective food-habits have mouthparts that are not so highly specialized; thus grasshoppers and cutworms have heavy mandibles for cutting vegetation; tiger-beetles and *Chrysopa* larvæ have sharp piercing mandibles. The whole structure of the predaceous animal, its "action system," is sometimes suggestive of the manner of pursuit or holding of its prey.

2. *Physiological Characters.*—The physiology of animals of different food-habits differs materially. Physiological characters are not apparent, generally speaking, and are secondary to psychological characters. The range of food assimilable by the animal is usually much wider than that selected by it, as is seen when animals of selective habits take new kinds of food when the usual food is exhausted, often thriving seemingly as well as before.

3. *Psychological Characters.*—Selection of food is determined chiefly by behavior characters of the animal. These may be so widely variable that the animal will be virtually omnivorous, as in the case of crickets, or so narrowly restricted that it eats only a single species of plant or animal, as the leaf-beetle *Blepharida,* a sand-prairie insect eating leaves of the three-lobed sumac, and the pentatomid bug, *Perillus,* which feeds on *Blepharida* (cf. *E:* 49, 30). Selection is only one of the many psychological characters relating to food. The behavior characters manifested in obtaining food are of great variety.

With these are accompanying structural and physiological characters, which, however, play a subordinate part.

4. *Biographical Characters.*—These may consist in timing the life-history of the animal with that of the food-species (plant or animal) in such a way that the period of greatest activity of the former coincides with the period of greatest growth or abundance of the latter. This feature may be incidental to seasonal change of physical environment. Whatever its cause, it is very general in an established association, so general that it is seldom recognized. It is of advantage to both animal and food species.

5. *Numerical Characters.*—The rate of reproduction must be so adjusted to its food-supply (plant or animal) "that only the unessential surplus of this food shall be appropriated, leaving the essential maximum product undiminished" (Forbes, 1909: 293). Species of restricted food-habits must remain less numerous in individuals than general feeders, as the available food-supply is very much less.

(II) *Characters Which Remove the Animal from the Competition of Other Forms*

1. *Structural Characters.*—Structures which permit animals to live in varied habitats, to take varied foods, or to time their activities differently, remove each group of animals from competition of all the others, resulting in advantage to all. To that extent the fossorial forelegs of the mole, the long proboscis of the butterfly, and modifications of the eyes of nocturnal animals, are characters which do away with competition. The structural characters are, however, accompaniments of modifications of behavior, and are secondary to the latter.

2. *Physiological Characters.*—Ability to digest food-materials unavailable to other animals is an advantageous physiological character. Thus the leaf-beetle *Chrysochus auratus,* which lives on dogbane (*Apocynum*), and the "skin-beetle" *Trox,* which eats animal tissues in an advanced stage of decomposition, have few com-

petitors for food. Physiological, as well as structural, characters, are accompaniments to modifications of habit.

3. *Psychological Characters.*—Apparent preference for certain activities, certain habitats, or certain foods, together with peculiar behavior complexes, seem to be of greater importance in removing animals from competition than structural and physiological characters. Highly regulatory habits permit certain animals to adjust themselves to changing conditions of competition.

4. *Biographical Characters.*—Professor Forbes (1909: 295–298) discusses the alternative timing of the active period among close competitors for food. (It so happens that the animals mentioned, having almost identical habits, compete with each other in many ways, besides with respect to food.) In the sand prairie it has been found that different species of certain genera, having otherwise the same habits, differ greatly in life-history. Evidence of this biographical adjustment is more or less complete for two species of *Arphia* (*E:* 21), two or three species of *Hippiscus* (*E:* 21), two species of the milkweed beetle, *Tetraopes* (*E:* 47), and three species of *Proctacanthus,* robber-flies (*E:* 55). In these genera the term of activity of one species is abruptly followed by that of another, the successive periods usually covering most of the summer season.

5. *Numerical Characters.*—When a certain limited food, place of abode, or other desideratum is used by two or more kinds of animals at one time, a numerical adjustment is likely to be found among these competing species. The rate of multiplication of each species must be sufficient to keep up its numbers, to allow it to hold place with competing species. (Too high rates of multiplication, on the other hand, are disadvantageous because of other influences.)

(III) *Protective, Defensive and Concealing Characters*

1. *Structural Characters.*—Animals have various defensive, protective and concealing structures. Stings, beaks, mandibles, teeth, claws, hairs, spines, resemblance

to surroundings in color or form—all are of advantage to animals which possess them. Certain of the interstitial or blowsand animals resemble in color the sand on which they rest (*Cicindela lepida, Stachyocnemis, Psinidia, Spharagemon;* cf. *E*).

2. *Physiological Characters.*—Malodorous and ill-tasting animals are to a considerable degree exempt from attack. This is essentially a physiological modification, though a structural basis in the form of glands may be present. In the sand prairie *Chrysopa* (lace-winged fly), a number of *Hemiptera,* ladybird beetles, soldier bugs (*Chauliognathus*), blister-beetles (*Epicauta*), and others, are ill-tasting (perhaps not to some animals). The skunk's lack of caution is well known.

3. *Psychological Characters.* — Self-preservation in animals depends more upon their activities and behavior than upon special structures. The ordinary methods of resisting or evading attacks of enemies are generally known and need not be discussed. Many specialized instincts have arisen, such as feigning death, or dropping to the ground when disturbed, as seen in many herbicolous beetles.

4. *Biographical Characters.*—It is to the advantage of animal species preyed upon by others if their period of greatest abundance is timed with the period of greatest activity of the animals which feed upon them.

5. *Numerical Characters.*—Animals, as well as plants, must produce a normal excess in numbers which will provide food for other animals and still leave a sufficient number of individuals to continue the species.

It will be noted that the various kinds of characters usually accompany one another, all being parts of a single modification. This modification may have relation to one or to several of the environmental influences (physical, plant or animal) or to more than one kind of antagonistic relation between the animal and others. The modification is not necessarily advantageous to the animal with respect to all or to any features of the environment, though a large number of characters do result in advantage. Characters advantageous in one relation may be disadvantageous or indifferent in another relation. The origin of the characters is not at present a subject which can be treated in a study of interrelations of organisms (cf. Shelford, 1912*b*: 342). Behavior characters appear to be of greatest importance to the animal in determining its relations with other organisms of the association, though usually these are accompanied by physiological or structural characters. The animal is not *adapted* to a particular status in the association; its ecological constitution determines what place it shall be able to find among the other animals of its surroundings. The relations among the various animals, when a state of equilibrium has been reached, are the result of mutual accommodation on the part of all the animals involved.

D. INTERNAL ACTIVITIES OF THE ASSOCIATION

It has been indicated that the complex of activities within the association is the synthesis of all the activities of the individual organisms. Each plant and each animal is subjected to physical, plant and animal influences. From the extreme complexity of the entire system of relations within the association, it is hardly possible to consider more than one or several of these at one time.[3] It is possible, however, to see that each species finds a status within the association, according to its particular combination of internal and external relations. It continues in fairly constant numbers from year to year. A change in these numbers, if at all great, may cause a disturbance in the association, which is quickly regulated by the activities of conflicting organisms (Forbes, 1880). The entire association of plants and animals, by very

[3] Very helpful diagrams are given by Shelford (*C*: 167, 168) which illustrate the food relations of land (prairie) animals. There are also diagrams showing food relations of aquatic animals (*C*: 70, 71). Food relations of animals of plains and mountain streams are discussed by Ellis (1914: 122–127; diagram on p. 125). References to studies dealing with interrelations of organisms may be found in the recent handbook of Adams (1913: 123 et seq.).

reason of the conflicting interests, the varying conditions necessary for existence, and the varying methods of response to these conditions, forms a self-contained and self-regulating system of activities.

III. RELATIVE INFLUENCE OF DIFFERENT ORGANISMS WITHIN THE ASSOCIATION—DOMINANCE

The plant ecologist determines which plants in an association are of greatest importance (dominant) by observing which species tend to increase at the expense of others, which are most abundant, most frequent, largest, etc. Competition among plants in a grassland association is mainly for space, and the dominant species are usually determined with considerable accuracy after some study. With the animals the consideration of dominance involves greater complexity. The important relations between conflicting animal species are those in which they obtain food, are removed from competition, or escape enemies. These relations are in each case most directly concerned with food. The plant-eaters of the association thus form a dominant group within the association, since predaceous and parasitic animals, and scavengers in large part, depend upon them for existence. Individual species within the various food-groups, however, present such striking differences in importance, that we can not speak of all plant-eaters as dominant forms, or that all animals of other food-habits are unimportant. It is merely probable that the phytophagous group will contain a larger proportion of dominant species. This appears to be the condition in the bunch-grass association.

A. Factors of Dominance Among Animals

The success of an animal species within an association is due to the resultant effect of a large number of factors. Among these may be mentioned number of individuals, size, activity, voracity, concentration of food, rapidity of growth, rapidity of reproduction, and wideness of distribution in space and in time. Dominance signifies more than mere ability of a species to thrive in its surroundings: the species of greatest influence are those on which the greatest number of other animals depend; thus dominant species are successful, but successful species are not always dominant. Species which are relatively free from competition or which have comparatively few enemies may be successful, but are not dominant, and are usually not numerous. Species which are successful and at the same time extremely abundant, usually form the food of a large number of other animals, as it appears to be the rule that no considerable source of food within the association is left unused. Dominance in a species, then, would seem to include the dependence of other animals upon it, plus the ability to thrive in spite of the drain upon its numbers.

B. CRITERIA OF DOMINANCE AMONG ANIMALS

The factors mentioned as contributing to the success of a species, and the numbers of animals dependent upon the species, are all indications of the degree of its dominance. It appears that another criterion is available, which perhaps expresses the summation of many factors which contribute toward dominance. This is the degree of specialization exhibited by the species in its adjustment to a particular place in the association. Dominant animals appear to be those of moderately specialized habits rather than those of highly specialized, or relatively unspecialized, habits.

C. SPECIALIZED AND UNSPECIALIZED ANIMALS

Each species may be referred to a position in the scale of specialization in habit. The degree of specialization of the species is well seen in the food-habits, though all the habits are to be considered. The most abundant food in the sand prairie is plant material, bunch-grasses. The majority of the plant-feeders are adapted to eat herbage of nearly any kind: they are not restricted to particular species or particular parts of plants. They are non-selective feeders. Grasshoppers, cutworms and certain leaf-beetles are thus moderately specialized plant-eaters. There are also non-selective predaceous animals, as tiger-beetles and lycosid spiders, which eat any kind of small animal. These are also moderately specialized. The moderately specialized animals carry on the gross metabolism of the association; they constitute the dominant group, and include the dominant species.

Selective feeders belong with the highly specialized animals. In the bunch-grass association *Languria bicolor,* an erotylid beetle, bores in the stems of the composite *Cacalia* (Indian plantain), while *Lygæus bicrucis* (hemipterous) feeds on the same plant; *Perillus circumcinctus* eats *Blepharida rhois.* Others of the association eat selectively. The majority of parasites are greatly restricted in their selection of hosts. Such animals are particularly dependent upon special kinds of food, which in many cases are not available to general feeders. Highly specialized forms are thus enabled to avail themselves of opportunities denied to animals of generalized type; but while they avoid competition by the adoption of special kinds of food, or by special habit of some other kind, they lack the versatility of the less specialized animals, being unable to adjust themselves to changed conditions. They may, therefore, become abundant at times; but as they depend wholly upon one variable condition (perhaps the presence of a particular plant species, which may be quite infrequent) they never can become dominant species. Absolute numbers of the insects which live upon *Cacalia,* for example, are insignificant in comparison with such animals as the grasshoppers.

On the other hand, animals of relatively non-specialized habits would also be ineffective in the association, for whatever field of activity they were to enter, they usually would find already occupied by some animal better constituted for that activity. Such non-specialized forms would assume particular importance only when some animal on which they might feed should become unusually abundant. Few animals are really non-specialized in habits; many moderately specialized species, however, may on occasion turn from their ordinary activities, perhaps to appropriate a particularly abundant kind of food. Many ants are thus habituated to certain ordinary kinds of food, but are able to eat organic food of almost any sort, and do vary their food with circumstance. When, as frequently happens, some animal species becomes very abundant,[4] the attacks of a great many species of flexible habits becomes concentrated upon it, and the numbers of the food-species are soon reduced to normal. Animals with non-specialized habits, by taking whatever food is easiest of access, act as regulators of disturbances within the association. A clear exposition of the manner in which species of generalized habits restore unbalanced conditions to equilibrium is given in a paper by Forbes (1883), in which the regulative action of birds upon insect oscillations is discussed.

The animal's status within the association is determined not only by its food-habits, but by the sum-total of its physiological and behavior characters (its mores). The degree of dominance is indicated not merely by the degree of specialization of food-habits, but in all habits, by the degree of flexibility of behavior. An extreme specialization in nearly any behavior character, as habit of abode in the pit-digging ant-lion larva, prevents the species from becoming dominant. The degree of specialization of behavior is thus a convenient criterion of the relative influence of animals in the association. The dominant animals are moderately specialized, and carry on the ordinary work of the association. The highly specialized animals make use of space otherwise unoccupied and food material not demanded by other species. Certain of the first group, with habits more highly regulatory than is usual, with perhaps some few unspecialized forms in addition, tend, by following the path of least resistance, to act in opposition to forces tending to destroy the biotic equilibrium.

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[4] With some animals sudden abundance is a matter of seasonal periodicity, as in the case of May-flies (Hexagenia) along the Illinois River (*E*:17). The adults on emerging become a sudden source of food for animals of adjoining terrestrial associations, as the bunch-grass.

IV. DISTRIBUTION WITHIN THE ASSOCIATION

The association may be subdivided into minor groups of organisms, both in space and in time. Each group, being thus removed from the immediate influence of the others, is to some extent self-contained, having its own environmental conditions, its own assemblage of organisms, and its own system of interrelations.

A. DISTRIBUTION IN SPACE[5]

Different parts of the space occupied by an association present different environmental conditions. In the vertical distribution, four strata, the air (cf. *E:* 73), the plant layer, the surface layer and the underground layer, are usually present. In forest associations, the plant layer is complex, plants of various heights giving rise to minor strata (cf. *A*). In grassland associations the plant layer is relatively uniform. Animals are most numerous, during the feeding activity, in the plant layer. Others find food at the surface or underground. Many of the animals in the air or on the ground move about rapidly from plant to plant. Predaceous animals (while active) are frequently permanent members of air and ground layers, depending for food upon the transient animals and upon members of their own group. The ground stratum is composed of the surface and subsurface layers (*E:* 72), which are not, however, continuous horizontally, but alternate to greater or less extent.

Local variability in horizontal distribution is due partly to local discontinuity of the various strata. This interruptedness is particularly conspicuous in open associations, where the plants do not form a dense growth, but are separated by open spaces. The subsurface area is provided by cover of various kinds, which lies more or less scattered about on the surface.

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[5] Cf. Shelford, *A*, *B*, 1912*b*, *C*; also *D*: 167; also p. — of this paper.

The motility of the animal allows change in stratum, and to some extent and in some animals, in habitat, with change in activity. The food-stratum and the food-habitat are apparently of greatest importance in the relation of the animal to other organisms.

B. Distribution in Time

Physiological activities of the plants are subject to diurnal variation, and are also greatly affected by variations in weather conditions. The greater part of the animals of an association are active during the day. Others are nocturnal. During the inactive period of the day the animal rests in some more or less sheltered place, perhaps in a burrow or nest. The inactive state is also induced by unfavorable weather conditions.

Seasonal changes in the association are very great in temperate climates, particularly in treeless regions, where the winters are severe. Seasonal changes in the vegetation are marked, certain groups of the plants appearing in successive periods during a summer season, giving four or five successive *aspects* to the plant cover. A corresponding seasonal distribution is observed among the animals of the association (cf. *D:* 175).

Annual changes in the associations are indicated by the very marked differences in the numbers of individuals, in certain species of plants and animals, in successive years. This may be due (1) to fluctuation in the numerical adjustment between different organisms, and (2) to the effect of annually varying phenological conditions upon the various organisms.

Oscillatory irregularities in the association take place at indefinite intervals. The causes and nature of oscillations have been thoroughly treated in several of Forbes's writings (1880, 1883, 1887).

V. INTERDEPENDENCE OF TERRESTRIAL PLANT AND ANIMAL COMMUNITIES

The thesis of the following section is that, in terrestrial climatic or extensive environments, the relations between the assemblage of plants and the assemblage of animals are intimate and regular of occurrence; so much so that (1) the two are coextensive, (2) the two constitute together a community which may be called a biotic association, (3) neither plant nor animal assemblage usually occurs independently of the other, (4) the geographic distribution of many of the plant and animal species which make up the assemblages are in general correspondence, (5) the species composition of the association, over its range, varies no more widely, relatively speaking, than would an assemblage of plants alone. Perhaps the single view-point of the botanist, on one hand, and the zoologist, on the other, has tended to a neglect of the dual character of the one problem. Probably most botanists and zoologists agree that relations of animals and plants within a habitat are most intimate, and there is a tacit assumption that all the organisms in one place constitute the true system of interrelations, but botanists have spoken of plant communities, and zoologists of animal communities. There are numerous disharmonies and variations in agreement of plant and animal assemblages, but these must not be allowed to obscure general facts of correspondence.

It is recognized that plants and animals of an area of essentially homogeneous physical conditions are interdependent, the animals as a group being wholly dependent upon the plants for food, and many of the plants being directly dependent upon animals, as in the matter of pollination. All are directly or indirectly affected by animals in some way. It is also recognized that the plants are a good index to conditions for animal life, the plant assemblage affecting animals locally in modification of the physical environment, and more directly in providing food, shelter, etc. (*A:* 601). It is further accepted that plants and animals respond to general environmental conditions in similar manner (Craig, 1908). Thus considered, the character of the plant population of an area is an index to general character, or ecological type, of the animal assemblage. These relations, however, are quite general, lacking detail. Detailed considerations may be *geographic,* including geographic range of species and of communities, and the distribution of species and of individuals into communities; and they may also be *local,* dealing with interrelations of plants and animals within the area of the community.

A. GEOGRAPHIC RELATIONS OF TERRESTRIAL PLANTS AND ANIMALS

1. *Geographic Range: The Province.*—If one were to plot the geographic range of the plant species found together in a given climatic habitat, a general correspondence in distribution would be made apparent, a large number of the species ranging more or less continuously over a common, rather definite area (cf. Transeau, 1905). The similar ecological constitution of these plants and their consequent selective distribution into similar environmental complexes gives a uniformity to the vegetation over the geographic region in which these environmental conditions are found, and the resulting vegetation unit is known as a *vegetation province* (Gleason, 1910: 42). The area of the province is generally uniform in physical conditions. This uniformity is only relative, being subject to gradual geographic variation in climate, perhaps giving rise to subregions in distant parts of the province, and to abrupt local variations in soil, water-content, exposure, etc., giving rise to local or edaphic plant assemblages very different from those of the climatic or geographic type. Thus the prairie province occupies the winter-dry interior region of North America. Environmental variations from east to west, climatic and physiographic, divide the province into the three subregions of Pound and Clements (1898). Certain plant species range over one or all of these subregions, still others establishing themselves over the whole area of the province and also scatteringly eastward, in dry treeless parts of the deciduous forest province, to the Atlantic coast. These last are also typical prairie plants, though

extra-limital in parts of an adjoining province locally approximating the prairie environment.

The habitat-selection of different animal species results, in precisely the same manner, in similarity of geographic range among ecologically similar animals. These correspondences of distribution point to the existence of definite areas characterized by general similarity of the animal assemblages. As the physical factors of the environment are the same ultimately for animals as for plants, and as the vegetational environment for animals has the same range as the physical environment, we might expect animal communities to have the same geographic distribution as plant communities, and we might expect the area of the plant province to be characterized by distinctive kinds of animals as well as by distinctive kinds of plants. The province is thus not simply a vegetation province, but a *biotic province*. This is not a new notion. Ruthven (1908: 388–390) has stated a current viewpoint as follows:

> Those who are acquainted with the literature of the field zoology of North America are familiar with the fact that, since the time of the Pacific Railroad surveys, naturalists have noted that there are in North America well-defined biological regions. These have been pointed out at various times by Allen, Cope, Merriam, and others, and the fauna of each has been more or less investigated. . . . For example, we have forms of birds, reptiles and mammals characteristic of the southeastern deciduous forest region, and still others characteristic of the northeastern coniferous forest region, etc.

Shelford (*A:* 604) bases his classification of animal regions upon that of plant regions, as worked out by Schimper (1903) and Transeau (1903, 1905).

How close the correspondence of distribution of particular animals with that of vegetation provinces may be, is well shown in the case of North American rabbits (Nelson, 1909). The distribution maps shown for certain species and groups of these animals might almost serve as maps of the provinces. Many other animals, vertebrate and invertebrate, correspond in area with the plant provinces. Among the insects listed by Hart (1907: 205) as western species, those for which a number of locality records are available are plainly to be assigned to the prairie province, the range of most of them extending west to the Rocky Mountains, north about as far as Montana, east to Illinois or Indiana, and south to Texas.

Other animal species bear apparently no relation to province boundaries. Such animals have been discussed by Shelford (*A:* 606, footnote), who shows them to be of three types: (1) Species of scattered but very wide range, covering perhaps several plant realms (animals of local associations of extreme habitats); (2) Species occupying only a part of the plant realm in which they belong (animals of such ecological constitution that their range is restricted by some conditions unfavorable in certain parts of the province); (3) Species occupying intermediate ground between two realms—these are few (Ruthven). These exceptional species are found also in plants, so that local associations are occupied by both plants and animals of the scattered-but-wide type of range, while certain subregions, as the Great Plains area of the prairie province, contain associations with both plant and animal species restricted to these less extensive areas.

Associations of two adjoining provinces may intergrade, if ecologically similar, or may alternate if dissimilar. Similar associations of two provinces may contain the same or closely related species, as with certain grasshoppers which range in both northeastern and western coniferous provinces (*D:* 173). But these same associations contain also plant species in common, so that irregularities of range are no greater in animals than in plants.

2. *Distribution Within the Province: Distribution of Plants and Animals into Communities.*—It is seen that plant and animal species may correspond closely in geographic range. There may be also more local correspondence in distribution. The plant community has been found by the writer to be the convenient index of the

area of the habitat for animals. It has been observed, in an area in Michigan, that grasshopper species correspond closely in local distribution with plant communities (*D*). There is evidence that local distribution of animals is seldom promiscuous as a result of motility (*D:* 159). It appears also that the local variability of environmental conditions within the area of the climatic plant community is sufficiently great, usually, to supply all necessary conditions for a large number of animals, so that the limits of the plant community need not be passed, ordinarily.

> The animal community of the area may be thus, in large measure, self-contained, and coextensive with the plant community (*D*: 161).

One of the problems of plant ecology has been the differentiation of plant communities or associations. Mere comparison of lists of species is not sufficient; relative abundance of various species must be considered as well. Animal assemblages in contiguous areas must be separated in the same way. Given two adjoining habitats differing in plant population, it has been found that, in addition to differences of animal species,[6] there are also differences of relative abundance in those animal species common to the two areas (*D:* 154, 167).

The local area of a plant community is determined by (1) local distribution of the physical environmental complex, and (2) influence (competition, etc.) of adjoining plant communities. Local area of the animal community depends upon (1) local distribution of physical environment, and (2) local distribution of vegetational environment, the latter being uniform over the area of the plant community. Contiguous areas differing in physical and vegetational conditions will be expected to differ also in animal population, in a degree comparable to that of the differences in environmental conditions.

Physical habitats, and plant communities, sometimes alternate, sometimes intergrade; it is not unreasonable to expect accompanying alternation or intergradation of animal populations. Certain of the animal assemblages of sand habitats, as studied in central Illinois, intergrade; others, as oak forest and bunch-grass, differ radically.

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[6] Differences in *species,* both plant and animal, are accompanied by differences in ecological constitution.

The above considerations, if correct, appear to signify that, in ordinary climatic development of plant and animal life in temperate land environments, the area of the animal assemblage is that of the plant assemblage, both resting basically upon the physical environment. The plant and animal assemblages are therefore coextensive parts of a biotic association, composed of both plants and animals, and this association as a whole constitutes the real terrestrial community of living organisms.

B. LOCAL RELATIONS OF PLANT AND ANIMAL ASSEMBLAGES (RELATIONS WITHIN THE ASSOCIATION)

The more intimate relations between plants and animals are seen in the detailed study of a single association. The bunch-grass association of sand prairie is selected for illustration (*E:* 68).

1. *Similarity of Ecological Type of Plants and Animals.*—Shelford has shown (*A:* 593–594) that animals and plants may evince ecological similarity by similar response to the same general environmental conditions, behavior responses in animals[7] corresponding to structural responses in plants,[8] so that *mores* of the animal may be in accord with *growth-form* in the plant. Shelford states (*B:* 87) that "plants and animal communities are in full agreement when the growth-form of each stratum of the plant-community is correlated with the conditions selected by the animals of that stratum."

In the bunch-grass there is general agreement, according to this criterion. The herbaceous stratum is occupied mainly by tuft and mat plants—bunch-grasses, cactus and a few half-shrubs. Associated with the tuft or mat growth-form is the sedentary mores of the plant-inhabiting animals (leaf-beetles, stem-borers, ambush-bugs, etc.). A considerable proportion of ground surface is bare sand; in the interspaces between the dominant plants are slender annuals (interstitial plants), and here are also found animals of the roving mores of the ground stratum (interstitial animals). Many of these are swift-running and predaceous (six-lined lizard, tiger beetles, lycosid spiders).

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[7] Or motile organisms, cf. *C*: 305.

[8] Or sessile organisms.

Correspondence in ecological type of plants and animals in the bunch-grass is not complete in several respects. Shelford mentions types of disagreement (*B:* 88; *C:* 306–308), and there is a further important kind of disharmony, in mixed associations, due to presence of diverse types of plants and animals (*D:* 163). Mixed associations are quite frequent in forest border regions, and in the transition area between two provinces. The plant and animal assemblages of a given habitat, particularly if climatic and extensive, are usually in general ecological agreement, and the exceptions are likely to be infrequent or temporary (Shelford, *B:* 88).

2. *Relative Dependence of Plant and Animal Assemblages.*—There is evidence that the agreement of plant and animal assemblages of terrestrial associations is often a matter of accommodation on the part of the animal assemblage. In the early stages of development of vegetation, local physical conditions dominate; in later stages the vegetation assumes the type determined by climatic conditions, and exerts nearly complete control over local physical factors. In established associations, therefore, the locally dominating environmental feature is the vegetation. Shelford states that in the several associations of a successional series, the dominating animal mores are correlated with the dominating conditions (*B:* 94) and that, as the forest increases in density, the animals make use of the vegetation in increasing degree, particularly for breeding-places, and as places of abode (*B:* 90). Many grasshoppers of open grassland depend upon a particular kind of soil for egg-laying, while those of closed forest lay eggs in fallen logs—a condition of the plant environment (*D:* 163).

The sand-prairie vegetation is in an intermediate stage, certain animals depending chiefly on the presence of loose bare sand, others on the bunch-grass vegetation. With development of bunch-grass into closed grassland, the interstitial animals are eliminated. The animals of established associations, while in accord with climatic physical conditions, are perhaps more intimately affected by vegetation conditions. Since established associations are very much more extensive than primitive associations, the importance of vegetation as a dominating part of the environment for animals becomes apparent, and we may conclude that the character of the plant assemblage determines, to a large extent, the ecological type of the animal assemblage.

3. *Correspondence in Distribution within the Association.*—The uniformity of physical and vegetational conditions is only relative. There are spots in the bunch-grass association in which local invasion of blue grass has occurred, darkening and binding the soil. In such partly humified situations, small colonies of the corn-field ant, not occurring elsewhere in the bunch-grass (*E:* 57), have been found. There are also areas some few feet in diameter in which the bunches of grass are few, small and scattered. In these relatively bare patches the abundance of interstitial animals is greatly increased. More direct relations are seen in the case of animals associated with particular species of plants. Within the association, any animal species, like any plant species, may be distributed generally throughout the area, or it may be restricted to a part of the area characterized by a slight environmental difference, or it may occur in scattered parts of the association, characterized by scattered local differences (*D:* 168). There is evidence that, in so far as the vegetational environment is concerned, distribution of animals within the association is usually a direct function of similar distribution of plants.

4. *Uniformity of Species Composition of Plant and Animal Assemblages.*—It has been seen that plant assem-

blages of definite ecological type, as regards growth-form, etc., are regularly accompanied by animal assemblages of similar ecological type, as regards mores. Interest attaches also to the problem whether associated plant and animal assemblages show definite *species* relations.

One familiar with a certain association, who visits a representation of that same growth in a different part of the same climatic region, will be struck with the fact that a large proportion of both plant and animal species is well known, while a certain proportion, perhaps considerably smaller, is new to him. The writer has been impressed with the similarity of the plant and animal populations of the sandhills of central Nebraska and of eastern Colorado, to those of the sand prairie of central and western Illinois, despite the fact that certain species are not common to the two areas. Tiger-beetles, blow-snake, grasshoppers, box-turtle, six lined lizard, western meadow-lark, white-footed mouse, among the animals; prickly-pear, lead-plant, bunch-grasses, sand-bur, sand evening primrose, among the plants; are represented in the two areas either by the same or by closely related varieties and species. There are no yuccas or sand-sages in the Illinois sand prairie, no lizard *Holbrookia* nor lubber-grasshopper *Brachystola;* and there are certain eastern species not found in the western sandhills. But on the whole the species (particularly the important species) common to the two areas are more numerous. This is the more remarkable in view of the fact that distribution of sand prairie is discontinuous, the largest, nearly uninterrupted gap being several hundred miles in extent. Many of the animals, as well as plant species, of dry mixed prairie-grass in loamy soil, are the same along the mountain-front in Colorado (Vestal, 1914*b*) as in north-central Illinois. The likenesses become much more impressive as distance is decreased.

Absolute identity of species composition, where large numbers of species are involved, is an ideal condition, never actually attained. No one can say just what proportion of species-in-common is necessary for two growths to be said to represent the same association. In addition to likenesses and differences of environment, of aspect, and of history, which must be weighed, the different plant and animal species vary so much in importance in the association, in physiological variation and in range of environmental tolerance, that associations can hardly be separated or placed together on a statistical basis. A comparison of species is fair if the following kinds of plants and animals are left out of consideration; (1) those of limited range within the climatic region or province, including species belonging more properly to other provinces; (2) those of very indefinite habitat-relations, which are found in nearly any kind of habitat; (3) those of special restricted habitats, which may be scattered about in many kinds of associations, as moist dead wood, in which particular fungi, beetles, perhaps snails, myriopods and pill-bugs, are usually found; or as excrement of grazing animals, in which certain molds, certain dipterous and scarabæid larvæ, etc., regularly occur, irrespective of surrounding conditions; (4) invaders from nearby associations; (5) ruderal and introduced species; and possibly one or two other groups. The second and third groups may be called the irregular element; the fourth and fifth may be known as the derived element. While these groups make a formidable list, their representatives constitute usually a very small proportion of the organisms of the association. The other organisms, and some of these, follow habitat-differences, as represented in different associations, very closely.

Since hardly any two species are identical in habitat-relations, geographic and even local variation must be looked for, but since many species resemble each other more or less closely in general ecological relations, there come to be recognized certain ecological groups of species, each characterized by a general type of growth-form in plants, or by a general kind of mores in animals, and these groups may be considered to be small or large, according as we emphasize minor differences or general likenesses.

Now within any limited region (let us postulate first an area removed from the influence of an adjoining province) there are only a limited number of ecological groups, of growth-forms of plants, and of mores among animals, each group represented by a limited collection of species. Each habitat within this restricted area will be characterized by definite physical conditions, and with these will be correlated certain growth-forms of plants and certain mores of animals, each represented by as many of the species as can migrate into and survive within the area, as determined first by capabilities of migration and by habitat-selection, and second by interrelation of species and of individuals. It follows that physical complexes which are alike will become populated with similar complexes of ecological groups, represented by similar collections of plant and animal species, and that unlike physical areas will be occupied by different combinations of ecological groups, and will be composed of different species. Two areas within this region which have similar physical conditions and similar plant growths will be expected to have a large number of animal species in common, although direct relations between species of animals and species of plants obtain only rarely (between comparatively few associated plant-and-animal pairs). It is to be noted that species composition of the animal assemblage varies proportionately no more widely than does that of the plant assemblage.

No terrestrial continental region is sufficiently isolated to be free from influence of surrounding areas, and since the influences are different from different directions, and since there is continual change of physical conditions, and of range and abundance of plant and animal species, there must be more or less local and geographic variation of species composition within similar but separated habitats. Geographic variation is wider with distance.

because the geographic and physiographic complexes vary geographically, as well as the entire collection of plant and animal species which may invade the habitat. Within the area of the climatic province, however, or at least within the area of a subregion of the province, climatic, physiographic and biotic complexes are likely to be relatively constant, that is, likenesses of two areas are likely to be greater and more striking than differences. Within the province or subregion, therefore, it is to be expected that species composition of association of closely similar habitats will be relatively constant. Particular plant and animal assemblages will be found together, both associated with a particular habitat. Field observation bears out these expectations.

Conditions within the transition zone between two climatic regions or provinces are much more complex than in an area in the middle of a sub-region or province; climatic and physiographic conditions vary to wider extremes and are less stable; the total number of species near enough at hand to invade a given habitat is much greater. Mixed associations, often transitional as regards physical conditions, are composed of representatives of both provinces. Animals of a particular association of one province, may be found with plants of a similar or equivalent association of the other province. When *three* geographic elements are represented, as at the southern end of Lake Michigan (cf. *C*, and Vestal, 1914*a*), the complication of conditions is extreme. Even here, on the dry sand of old lake beaches, fairly typical representations of sand prairie can be seen; and though such habitats are shared with deciduous forest associations, and with associations of the northeastern coniferous forest province, and with mixed associations, the bunch-grass growth can still be recognized in dry shifting sterile sand, with bunch grass plant species, and bunch-grass animal species. The tendency towards uniformity of association of plant and animal assemblages is even here to be made out.

If the foregoing considerations relating to relations between plant and animal communities are correct, the thesis mentioned at the beginning of part V would seem to be justified, though the evidence is far from complete. Plant and animal assemblages are mutually interdependent; the plant assemblage dominates in established associations. Plant and animal assemblages correspond in geographic distribution, in distribution into communities, and in more detailed distribution within the habitat. They are made up of ecologically similar groups correlated with the same physical conditions or with each other. Though there are few direct relations between particular species of plants and animals, it so happens that within any restricted region, particular collections of animal species come into regular association with particular collections of plant species, the species composition within the habitat exhibiting a greater or less degree of uniformity, except for minor irregular and derived elements. The more restricted, or uniform in biological conditions, this region is, the greater the uniformity of the collection of species. Climatic and extensive associations, and established associations, show a greater degree of uniformity than local or primitive associations.

VI. SUMMARY AND CONCLUSIONS

The discussion is based principally upon the writer's study of prairie associations, the bunch-grass association of sand prairie in Illinois being chiefly used for illustration. Internal activities of the association are a complex of activities of all the organisms. Environmental influences are of three classes, physical, plant and animal. The characters of plants and animals are interpreted in their relation to these influences. Characters of plants may be classed as structural, physiological, biographical and numerical. Animals have, in addition, behavior or psychological characters. These groups of characters are intimately related, one to another. The relations of the animal to its animal-environment are of two kinds, social and antagonistic, the latter relations being with food-species, competitors and enemies. Correlations of the various kinds of characters with relations involving food, competition and enemies, are given. According to its ecological constitution, each organism finds a status in the association, the whole being a self-contained and self-regulating system of activities.

Dependencies within the association are concerned mainly with sources and interchange of material and energy. Dominant plants (the most influential species) are those most intimately correlated with physical environment, as indicated by aggressiveness, abundance, frequence, size, etc. Dominant animals are most numerous among phytophagous forms. Dominance in an animal species includes dependence of other animals upon it (for food) plus the ability to thrive in spite of the drain upon its numbers. The degree of specialization of behavior is a convenient index of the relative influence of animals in the association. The dominant animals are moderately specialized, and carry on the ordinary work of the association. The highly specialized animals make use of space otherwise unoccupied, and food material not available to other species, or not taken by other forms. Least highly specialized animals act as a check upon undue departure from biotic equilibrium.

The association may be divided into minor groups of organisms, both in space and in time. Space-division is vertical, resulting in strata, and horizontal, resulting in sub-habitats of greater or less magnitude. The strata and sub-habitats present a larger or smaller degree of discontinuity and of internal variability. Time-distribution is diurnal, seasonal and annual. There are also time-variations produced by variability of weather conditions and by oscillatory disturbances.

The relations between plant and animal assemblages have long been known, in a general way, to be intimate. Plants and animals agree in similar response to common environmental influence, and in types of geographic distribution. Upon investigation, it begins to appear that plant and animal assemblages are coextensive parts of a biotic association, composed of both plants and animals, and this association as a whole constitutes the real terrestrial community of living organisms. Plant and animal assemblages are mutually interdependent; the plant assemblage dominates in established associations. Plant and animal assemblages correspond in geographic distribution, in distribution into communities, and in more detailed distribution within the habitat. They are made up of ecologically similar groups correlated with the same physical conditions or with each other. Though there are few direct relations between particular species of plants and animals, it so happens that within any restricted region, particular collections of animal species come into regular association with particular collections of plant species, the species composition within the habitat exhibiting a greater or less degree of uniformity, except for minor irregular or derived elements. The more restricted in area, or uniform in biological conditions, this region is, the greater uniformity of the collection of species. Climatic and extensive associations show a higher degree of uniformity than local or primitive associations.

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